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THE VERTICAL DISTRIBUTION OF VOLVOX IN THE PLANKTON OF LAKE MONONA

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On the morning of July 6, 1916, Messrs. Birge and Juday, of the Wisconsin Geological and Natural History Survey, noted a very peculiar condition, while collecting plankton samples from Lake Monona, Madison, Wisconsin. They found that there was a very decided stratum of Volvox colonies at a depth of three meters, while above and below this stratum the colonies were very scarce. Mr. Juday called my attention to this condition, and suggested that I make plankton catches at various times of the day to see if the position of the belt changed. Although the data presented herewith are, at best, fragmentary, they seem worthy of record since nothing is known concerning the vertical distribution of Volvox as a limnetic organism. The "bloom" of this alga is so sporadic that it may be some time before so favorable a condition for a study of this kind again presents itself.

The ordinary method of pumping a measured amount of water (ten liters) from a desired depth and then straining through a filter net was used for collecting the samples, which were then preserved in alcohol until counted. In counting, the volume of the catch was reduced to ten cubic centimeters, then a one-cubic-centimeter sample was taken, put in a trough, and the number of colonies counted through a binocular microscope.

The station where the alga was first discovered is about a kilometer northwest of Winnequah point, at the deepest part of the lake. My samples were collected about a half kilometer out from the Wirka Boat Livery where the water is between ten and thirteen meters deep. This station is about a kilometer and a half from the deepest part of the lake. Sunset occurred at 7:40 on July 6 and the sample from the surface was taken at 7:45. Since it takes about five minutes to adjust the hose, pump the water, label and preserve the sample, the interval between two catches is about five minutes. The same order was followed in every case, the first sample taken at the top and others on down at intervals of a meter. Twilight lasts about an hour at this season so that it had been dark for nearly an hour when the next series of samples was collected at 9:20 P.M. The following morning the sun rose at 4:26 and the first catch was made at 4:25. A series of samples was collected every succeeding hour until 8:30 and then at 10:00 and again at noon. Collecting was resumed at 5:30 A.M. the following day and continued at hourly intervals until 9:30 A.M. when the sky became cloudy and a sharp squall blew up. The wind caused considerable wave action, so that what vertical distribution there had been was disturbed. The results of these collections are shown in the following table. Those of the last day's collecting are not incorporated since practically no colonies were found.

TABLE I

Number of Colonies per Liter at the Various Depths

Depth in Meters	July 6 (Evening)		July 7 (Morning)						
	7:45	9:20	4:25	5:30	6:30	7:30	8:30	10:00	12:00
0	890	1,900	670	11,500	10,100	8,600	13,800	14,300	28,100
1	1,200	820	10,810	12,400	15,500	24,500	19,300	13,300	14,600
2	4,390	1,620	5,840	17,500	5,800	12,500	10,900	5,230	2,100
3	33,200	2,300	9,600	7,700	1,670	2,130	1,280	3,560	980
4	2,790	11,300	3,150	1,290	650	590	1,250	840	510
5	—	9,010	810	—	—	—	—	—	—
6	—	3,980	—	—	—	—	—	—	—

The weather conditions, at the time the collections were made, are important factors. Had there been any wind stirring up the water the vertical distribution would have been affected. Since the 6th and 7th were exceptionally calm days this factor may be neglected. The following meteorological data have been furnished by Mr. E. R. Miller, the Local Forecaster of the Weather Bureau. The meteorological observations are taken at a point about forty-five meters above the level of the lake where there is always a greater air movement than on the lake surface. Shaw (8) gives methods of estimating the velocity of the wind so that the weather conditions of the 6th and the 7th may be easily visualized.[1] Both of these days were bright and sunny, the amount of sunshine being very near the maximum for this time of the year. The local office of the Weather Bureau records the total energy of the sun's rays in the form of calories per minute per square centimeter of surface. The curves for the two days are almost identical, so that no distinction can be made between the two on the basis of different light intensities. Table II gives the light intensities at the times that the samples were collected on the 7th of July.

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[1] When the wind is blowing at two miles per hour the direction of wind is shown by smoke drift, but not by wind vanes; at five miles per hour the wind is felt on the face, leaves rustle, and ordinary weather vanes move; while at ten miles per hour leaves and small twigs are in constant motion and the wind extends a small flag (p. 31).

TABLE II

Weather Conditions at the Time Samples Were Collected

Velocity of Wind			Total Sunshine (Morning July 7)	
Date	Av. Vel. in Miles per Hour	Max. Vel.	Hour	Cal. per Min. per Sq. Cm.
July 6..........	3.6	8	4:25	0.00
			5:30	0.12
July 7..........	4.2	8	6:30	0.39
			7:30	0.60
			8:30	0.82
			10:00	1.07
			12:00	1.28

Table I shows that the clearly defined stratum found on the morning of the 6th was still at a depth of three meters at sunset, when the sun's rays are less intense than in the morning. After sunset, however, the band was broken up, a majority of the colonies sinking from one to three meters. At sunrise on the following morning the colonies were in the upper three meters and as the day progressed they migrated toward the surface until at noon over ninety percent were in the upper meter. The data on this gradual rise vary somewhat from hour to hour, but these variations are, in my opinion, due to experimental errors and do not represent changes in the position of maximal distribution.

TABLE III

Table Showing Temperature Range for the Upper Seven Meters of the Lake

	Depth in Meters							
	0	1	2	3	4	5	6	7
Temp. in deg. Cent........	25.0	24.4	24.0	23.1	22.3	21.4	20.5	19.2

It is well known that Volvox responds to various stimuli. Changes in temperature, chemical composition of the water, direction of the force of gravity, or light may cause a change in the position of colonies. The following table shows the temperature variations for the upper seven meters of the lake on the morning of July 6. Thermotaxis is not a factor in the problem before us since the difference between the upper and lower range is comparatively slight, while the differences between day and night temperatures are negligible.

The variable factors of the chemical environment are the gases in solution in the water. Birge and Juday (1) have studied this problem of dissolved gases particularly on Lake Mendota, which flows into Lake Monona, and at that time the conditions in the two lakes differed but little. They find that the carbon dioxide occurs in two forms, the fixed ($CaCO_3$ or $MgCO_3$) which is not available for the photosynthetic activities of the plant, and the half-bound ($CaCO_3.H_2CO_3$ or $MgCO_3.H_2CO_3$) which is such a loose combination that it is available for the use of algae. When the free carbon dioxide of the water has been exhausted the algae draw upon this supply of half-bound carbon dioxide and this produces an alkalinity of the water. The degree of alkalinity in Table IV is measured by the number of cubic centimeters of carbon dioxide that would be required to convert the normal carbonates into bicarbonates and thus give the water a neutral reaction. This difference, or degree of alkalinity, is the measure of the amount of the half-bound carbonates that have been utilized by the algae. The data of Birge and Juday for July 10, 1906, may be taken as typical for midsummer conditions in Lake Mendota (Table IV). The table shows that the oxygen was practically constant in the upper five meters, the region from which Volvox was collected, while the extent to which the available supply of carbon dioxide had been utilized shows that there was comparatively little difference in the first five meters. There is then no especially localized density in the amount of photosynthetic material or oxygen to cause a localiza-

TABLE IV

Gases Dissolved in the Water of Lake Mendota (after Birge and Juday, 1, p. 158). The Data Are in the Form of Number of Cc. of Dissolved Gas per Liter

Depth in Meters	Temp.	Half-bound CO_2	Fixed CO_2	Oxygen
0	24.2	−6.6	35.9	7.0
5	20.1	−6.1	36.2	6.9
8	17.7	−2.0	36.4	4.0

tion of the alga in any particular place in response to a chemotactic stimulus.

Geotaxis, however, plays an important part in the distribution of Volvox. Mast (5) finds that, when a horizontal beam of light is thrown across an aquarium, the colonies tend to move horizontally towards the source of light, but the force of gravity pulls them downwards so that they sink very rapidly until, as a result of the difference in weight between the anterior and posterior ends, they become vertically oriented and begin to swim upwards. He also finds that after an aquarium has been in darkness some four or five hours many colonies are at the surface of the water. This probably explains the condition noted at 9:20 P.M. After sunset gravity is the only stimulus operating upon the colonies. Since they are heavier than water they tended to settle, and sank from one to three meters below their position at 7:45 P.M. Some time between 9:20 and sunrise the next morning the colonies became vertically oriented and swam upwards, so that at sunrise they were in the upper three meters of the lake. The physiological condition of the colony affects this upward swimming. Mast (5) observed that the colonies would be lying motionless on the bottom of the aquarium after standing in darkness for some hours. When illuminated they did not respond immediately, but after a while slowly began to move in all directions, later becoming normally active and moving towards the light. He applied the term "dark rigor" to describe their condition when lying on the bottom. Apparently there was no "dark rigor" in the Volvox colonies in Lake Monona since they were found in the upper part of the lake at sunrise.

Light is by far the most important factor governing the distribution of Volvox. The response to light by Volvox has been noted by many naturalists, but Oltmanns (7), Holmes (2) and Mast (5, 6) are the only ones to have made quantitative studies. Oltmanns produces a graded intensity in the illumination of an aquarium by passing a beam of light through a hollow glass prism filled with a mixture of India ink and gelatine. The narrow end of the prism permits most of the light to pass through while the broad end of the prism absorbs the greater portion of it. He finds that the colonies collect at a given light intensity, but if the general illumination of the prism is lowered, as when a cloud passes over the sun, the colonies move toward a region of formerly greater illumination. The experimental errors in this method have been analyzed by Mast (6). Holmes's studies are largely concerned with an attempt to explain the mechanics of orientation. He notes that Volvox is negatively phototactic in strong light, while in very weak light colonies exhibit no pronounced phototactic movement, lying quietly or rolling about sluggishly. The most extensive studies are those of Mast, whose "light grader" for producing a graded intensity of the illumination overcomes the experimental errors of Oltmanns' apparatus. His investigations center about the orientation of the colony with respect to the direction of the rays of light, and he concludes that direction of movement in a colony is determined by the difference in intensity of illumination of the two sides of the colony rather than by the colony placing itself in a specific position with respect to the rays of light.

The explanation of the formation of the stratum at a depth of three meters on July 6 seems to me to rest on a heliotactic basis. Several investigators have noted that Volvox is positively heliotactic in weak light and negatively heliotactic in strong light. The formation of this stratum was probably caused by the colonies moving into the region of optimum illumination in the same way that Oltmanns (7) found in his experiments. This condition remained fairly constant during the day. The fact that the stratum did not move upwards when the illumination decreased at sunset is, however, not in accordance with this view. The dropping of the colonies from the three-meter level after sunset has already been ascribed to geotaxis.

The condition found at sunrise on the following day has been explained by the tendency of colonies to swim upwards in darkness after the greater weight of the posterior end orients them into a vertical position. There is the possibility that heliotaxis had been operating for some time before the collection was made at 4:25 A.M., since there is considerable illumination before the sun actually appears. Three quarters of an hour before sunrise a man could not be distinguished at a distance of seventy-five yards. If, then, we ascribe this movement of the colonies to the surface to heliotaxis they must have traveled three meters or more during the half hour of faint illumination. It would be reasonable to assume that this rate of movement continued during the hours after sunrise; so, when we find that the colonies did not rise more than a meter between 4:30 and 6:30, it seems illogical to assume that the light before sunrise caused the change of position. This is especially true when we remember that Holmes (2) finds no pronounced phototactic movement of Volvox in weak light.

Table I shows that during the morning of the 7th there was a continued upward migration of the colonies until at noon practically all were in the upper meter. These results are wholly inconsistent with those of the previous day. The colonies were in the region of maximal sunlight where the amount of light was undoubtedly far in excess of the optimum. The measurements of the total illumination for the two days are practically the same, so that this movement cannot be accounted for on the basis of heliotaxis. It is a well-known fact that filamentous algae like *Spirogyra* rise and fall during the day because of a buoyancy from the adherent oxygen bubbles formed during photosynthesis. The suggestion that a buoyancy of this type may have carried the colonies to the surface is inadequate since the illumination of the two days was constant. The variation in the gases dissolved in the waters of Lake Mendota has been discussed above and the assumption made that present-day conditions are the same. During recent years the "sludge" from the city sewage disposal plant has been emptied into Lake Monona, and it is just possible that the oxygen requirements of the undecomposed sewage coupled with the lack of aeration in the upper five meters by wave action produced a deficiency of oxygen that caused the migration of the colonies into the region of intense illumination the second day.

The third day's investigations showed but few colonies. The length of the hose did not permit sampling below eight meters, but all depths to the bottom were sampled where the water was less than eight meters deep and few colonies were found where the previous day the shallow water had been a bright green. This disappearance of the alga overnight, while very remarkable, is not inexplicable. We know from the studies of Marshall Ward (3) and others that direct sunlight kills many algae. Mast (5) has shown that this is also true for Volvox. Since the colonies were in full sunlight on the 7th, it is not at all improbable that they were killed by this strong light and gradually sank to the bottom. We should therefore find no colonies on the 8th or on succeeding days.

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